

16. The Structure and Development of the Caudal Skeleton of the Teleostean Fish, *Pleuragramma antarcticum*. By A. KNYVETT TOTTON*.

[Received December 17, 1913: Read March 17, 1914.]

(Plates I. & II.†)

INDEX.	Page
Morphology	252
Development	254

In this paper I have recorded several points of interest in connection with the development of the vertebral column of a Teleostean fish, *Pleuragramma antarcticum*. My material consisted of a collection of the post-larval stages collected on the Southern Cross Expedition, and handed over to the Imperial College of Science for description on behalf of the Trustees of the Natural History Museum by Professor Jeffrey Bell, to whom I here wish to express my thanks. To Professor E. W. MacBride, F.R.S., V.P.Z.S., at whose suggestion I undertook this piece of work, and under whose supervision it has taken its present form, and to Mr. H. G. Newth, for very much useful help, my thanks are due and are very gratefully tendered.

Unfortunately the *Pleuragramma* material does not contain stages quite late enough to show the actual formation of centra, though the largest specimens are about 4·5 cm. long.

I believe that no specimens of this fish have been taken intermediate in size between those at my disposal and certain specimens—adults 16–17 cm. long, taken from the stomachs of Seals,—one of which Mr. Tate Regan very kindly allowed me to examine, together with a specimen of *Trematomus newnesii*, a closely allied species in which the notochord is relatively smaller and the centra better ossified than in *Pleuragramma antarcticum*.

The fixative used in most cases appears to have been formalin or spirit, so that the material is not very good from a histological point of view.

Pleuragramma antarcticum is a specialised Teleost of the family Nototheniidae, the genus differing from the related Antarctic genus *Trematomus* chiefly in the feeble ossification of the skeleton. Boulenger included *Pleuragramma* in the family Leptoscopidae, but Regan has pointed out that it does not resemble *Leptoscopus*, but, on the other hand, is very near *Trematomus*. Most of the Nototheniiform fishes are littoral and feed on crustaceans, molluscs, etc. *Trematomus newnesii* and *Pleuragramma antarcticum* are amongst the more southern types, and appear to be circumpolar (*cf.* Regan, Trans. R. Soc. Edinburgh, xlix. 1913, pp. 251, 257, 264, &c.).

* Communicated by Prof. E. W. MACBRIDE, D.Sc., F.R.S., V.P.Z.S.

† For explanation of the Plates see p. 260.

The caudal skeleton of an adult specimen of *Pleuragramma antarcticum* consists of a number of relatively large cylindrical bony centra of a papery nature. To the terminal one are attached two expanded hypural bones, whose development proves that they are compound (*i. e.* that they represent more than two), and a third ventral hypural which is not so expanded. Between the latter and the ventralmost of the former two hypurals, the terminal branches of the caudal artery and vein come forth on each side in a notch. This terminal centrum bears no arches, but lying dorsal to it and the nerve-cord (not represented in Pl. II. fig. 12) are two bones, the epiural apophyses (*cf.* Huxley, Q. J. M. S. vol. vii. p. 41). Development shows that there were originally three, and there are even indications of a fourth. The penultimate centrum at first sight appears to be carrying two neural and two hæmal arches, but in the case of the neural arches, at any rate, development shows clearly that they have arisen through the division of one cartilaginous "Anlage."

I should like to make a digression here to discuss at greater length this phenomenon of a centrum bearing two neural or hæmal arches. I have collected a few cases from various authors, and have observed the phenomenon also in a few specimens in which it has not been described, so far as I am aware.

Mormyrus kannume has two hypurals on the penultimate centrum (*cf.* Whitehouse, "Caudal Fin of Teleostomi," P. Z. S. 1910, p. 596). I am not aware that the development of this fish is known. It would be interesting to see whether the adult condition was brought about by a division of a single cartilaginous "Anlage" or by a crowding together and displacement of arches, as is more probable.

Lotz (Zeitschr. f. wiss. Zool. Bd. xiv. 1864, p. 88) gives the following description of *Cottus gobio*:—"Der vorletzte Wirbel hat nur das Eigenthümliche, dass sein oberer Dorn sehr breit und oben gespalten ist, so dass er aus zwei verschmolzenen Dornen zu bestehen scheint." The figure shows a much expanded neural and a hæmal arch on the penultimate centrum, and the neural arch shows a line of division into two. I think this is a clear case of "division." Moreover, "division" seems to be connected in some way with expansion, as comparison with other cases will show. He says of *Barbus fluviatilis*:—"Der drittletzte Wirbel besitzt in der Regel zwei obere Bogen deren Dornen bereits als Stützen der kurzen Flossenstrahlen dienen, diess ist übrigens nicht constant; es kann auch nur ein oberer Bogen vorhanden sein oder es kann der vorletzte Wirbel deren zwei besitzen, während er in der Regel nur einen besitzt, dessen Dorn mit einem knorpeligen Ende versehen ist" (p. 86). On page 95 he says of *Salmo salar*:—"Am. 17-18. Tag. wird über dem Neural-canal hinter dem letzten normalen oberen Bogen (*g*) der erste falsche Dorn (*k*) gebildet." The "falschen Dornen" are the epiural apophyses. It is to be noted that the neural and hæmal arches have already been formed. Lotz continues: "Oft

der vorleste der falschen Dornen mit dem Dorn des letzten oberen Bogen verschmilzt oder es ist ein ganzer überzähliger Bogen vorhanden, so dass dann der viertletzte Wirbelkörper zwei obere Bogen erhält." The "Wirbelkörper" appear towards the end of the fourth month, doing so first in front.

O. Hertwig ('Entwickelungslehre der Wirbeltiere,' III. II. pp. 456-82), in the account of the development of the vertebral column of Teleosts by Schauinsland, says:—"Finally, it must be pointed out, too, that there are vertebræ in the tails of many Teleosts, with fully formed and equally developed double upper (or also both upper and lower) arches, the cartilaginous rudiment of which can sometimes even be shown." It is not very clear what he means by the last statement. Does he mean that there is a single "Anlage" or that there are two? He continues: "These vertebræ can be regarded either as corresponding to only two sklerotome halves, in which case, however, the arches belonging to each half have become exceptionally developed to an equal extent, or (which is more probable) as having arisen by the later union of the two complete vertebræ; that is to say, at least three, perhaps even four, sklerotome halves participate. In these cases, then, there would be real (secondary) "Diplospondyly." He does not bring forward any embryological evidence to prove his case, except the above-mentioned statement of doubtful meaning. He refers to a figure (270) of the "Dorsch" (*Gadus morrhua*) as showing double upper and lower arches on the penultimate centrum, but I believe there is something peculiar about the caudal fin-skeleton of *Gadus* which has not been described, with reference to these double-arch bearing centra. I understand that the appearance is due to partial fusion of arches and radials.

I myself have met with the phenomenon of a centrum bearing double arches in the case of *Trematomus newnesii*, where there are two very well-defined neural arches on the penultimate centrum (see Pl. II. fig. 13); also in the case of *T. borchgrevinki* (see fig. 14), where, curiously, it is the antepenultimate centrum which bears double upper arches and double hæmal arches as well. The penultimate centrum has greatly expanded arches, and, indeed, there is some slight indication of a division in the neural one, but the specimen was a dried skeleton and one not entirely free from flesh, so that I had some difficulty in making an accurate observation. In *Notothenia macrocephala* the arches of both antepenultimate and penultimate centra are somewhat more expanded than the rest, but only the penultimate neural arch shows any sign of division. I examined a number of allied forms, but did not come across any more cases of centra with double arches. I may mention that my drawings of the skeletons of the adult *Pleuragramma antarcticum* and *Trematomus newnesii* were made from specimens dissected very carefully in spirit, and from which every particle of flesh had been removed, and as much connective tissue as possible also.

I will now return to my description of the caudal skeleton of *Pleuragramma antarcticum*.

One of the chief characteristics of this skeleton is the large size of the cartilages supporting the procurent rays. No doubt, this is connected with the weakness of general ossification. The caudal skeleton of an adult specimen of *Trematomus newnesii*, though generally similar to that of *Pleuragramma*, differs in several points. As mentioned above, the general ossification is much stronger. Correlated with this probably is the smaller relative size of the cartilages bearing the procurent rays. The epidual apophyses are three in number. The two terminal hypurals still retain something of their compound nature; finally, the penultimate centrum bears a well-defined double neural arch, but a single unexpanded hæmal arch. The free end of the notochord extends further, and that of the nerve-cord not so far as in *Pleuragramma*.

In specimens of *Pleuragramma antarcticum* of about 8 mm. (Pl. I. fig. 1), the tip of the tail and the notochord are bent slightly ventralwards, the angle thus formed being filled up by skleroblastic tissue (*sk*). This latter consists of mesenchymecells, in which the cytoplasm has become clearer and the nucleus more distinct (*i. e.* takes up stain more readily) than in the cells of the surrounding tissue. The continuous fin-fold round the tip of the notochord is expanded and supported by actinotrichia. Whether this bending down of the tip of the notochord is apparent in the living animals or not I do not know. It certainly appears in large numbers of fixed specimens. One is reminded, in connection with this, of the prolongation of the vertebral column into the lower lobe of the vertical caudal fin of the Ichthyosauria. I think the condition I have described can scarcely be due to fixation, because, since the skleroblastic tissue is denser than the tissue dorsal to it, the tendency of the fixative would be to shrink the upper tissue more than the lower, and so turn the tail upwards instead of downwards. I suggest that the presence of the skleroblastic mass under the notochord gives rise to some sort of stimulus causing this flexure. I should like to call attention to the fact that Ryder (U.S. Comm. of Fish & Fisheries, 1884, p. 1057), in describing the development of *Alosa*, says:—"Here the development of the hypurals is accompanied by a pressing inward of the ventral wall of the chorda." He gives a figure (fig. 2, pl. ii.) to illustrate his point. I think that the illustration would be more correctly interpreted as showing a ventral flexure of the chorda, since the dorsal wall of it is also involved.

In the next stage (.85 cm.) (fig. 2), the skleroblastic cells in the concavity of the notochordal flexure have become divided into an anterior and a posterior mass, and a hyaline matrix has been secreted around and between certain of them, and in this way three blocks of cartilage are formed, two in the anterior mass of skleroblastic tissue and one in the posterior mass. Lepido-

trichia (*lp.*) have also been formed at the margin of these blocks of cartilage.

Stage III (1.05 cm.) (fig. 3).—Darkly staining skleroblastic tissue (*sk'*.) has now made its appearance above the notochord immediately dorsal to what will later become the "ventral hypural" (*a.*). It is significant to note that just at this time the notochord is becoming straight again. This secondary dorsal flexure is started, I suggest, by some stimulus due to the appearance of this new mass of skleroblastic tissue. More cartilage has now been formed ventrally, in front of the two pieces already described (Stage II), in the anterior skleroblastic mass, which two pieces have probably fused to form *a*, fig. 3. This new cartilage consists of a pair of proximal pieces and a median distal piece. The former, *b*, represent a hæmal arch and the latter is a radial. That the proximal pair of cartilages represent, or are serially homologous with, the arches which appear later and more anteriorly seems probable, because they correspond well enough in size and in the manner of their appearance. I must confess that I am not quite satisfied that the proximal and distal parts are actually separated, as the appearance of the line of separation may be due to optical section. In any case, the fusion between arch and radial in the next anterior segment is quite clearly seen (figs. 5 & 6), so that the evidence for the fusion of the above-mentioned elements is presumptive.

One may regard these cartilages, perhaps, as being in a condition intermediate between that of the hypural behind, which apparently is formed from the skleroblastic tissue as fused arch and radial, and the condition of the arch in front, where fusion of the originally separate elements can be seen as development goes on. I may say here that the term "hypural" is limited to those pieces of cartilage (which may later become ossified) which represent or are actually made up of fused arches and radials. The hypural (*a*, fig. 3), behind the one whose development I have just traced, is a good deal larger than this latter, and is somewhat rounded when seen laterally. It is beginning to form an anterior peg which later on passes through the arch formed by the proximal end of the hypural next in front, and lies just dorsal to the caudal artery and vein which run in the arch. The caudal fin is now beginning to be constricted off ventrally from the median fin-fold.

Stage IV (fig. 4).—Examination of specimens 1.3 cm. long shows that the upturning of the notochord has gone on further, and produced from the straight condition seen in the specimens 1.05 cm. long one in which there is a distinct dorsal flexure. The epaxial elements (*ep.*), formed by the skleroblastic tissue mentioned in the last stage, lie in the concavity thus formed. The posterior hypural cartilaginous block (*phy.*) can now be seen to be made up of two partially-fused blocks, or, rather, the original mass of skleroblasts has secreted two masses of matrix, which are not completely divided the one from the other. Similarly, the hypural

in front (*a.*) is incompletely divided into two on the proximal side, showing that it represents more than one hypural. There is, in the specimen figured, a small piece of cartilage (*h.*) between the "posterior" and "anterior" hypurals. This would appear to be exceptional, and may be the vestige of another hypural. Hæmal arches are now beginning to appear anterior to the hypurals, developing from behind forwards. The matrix secreted by the skleroblasts diminishes in amount as one goes forward. The lepidotrichia are still better developed and extend to the margin of the fin. There is figured a row of lateral-line sense-organs on each side, which extends on to the future mid-line of the caudal fin, dividing the lepidotrichia into a dorsal and a ventral series.

Stage V (1.55 cm.) (Pl. I. fig. 5).—There are now three distinct (a rudimentary fourth) epaxial elements (whose appearance seemed to give the signal for the secondary flexure of the notochord). In transverse section they show no signs of forking at their proximal ends, and they originate from single median masses of cartilage, not from paired pieces as do the arches. They are much closer together than the neural arches, which are now appearing anterior to them, much in the same way as the hæmal arches arose. There is a gap between these epaxial elements and the neural arches. These elements, moreover, stand quite clear of the nerve-cord, not arching it over as the neural arches do. They probably correspond to Huxley's epidual apophyses in *Gasterosteus* (Huxley, Q. J. M. S. vol. vii. p. 41). The fusion between the neural arch and radial, described as possibly existing in Stage III, is now complete: there is no line of division between the matrix of one and that of the other. A slight notch has appeared in the posterior border, and it is here that the caudal artery and vein run out on either side. A radial (*r.*) at the distal end of the hæmal arch next anterior to the one just described has been formed at this stage, but no fusion of the two elements has yet taken place.

In Stage VI (1.8 cm.) (fig. 6) there is still no sign of the cartilages to which the procurent caudal fin-rays are attached in the adult. A typical neural arch, taken further forward than those shown in fig. 6, extends at this stage through a length of about 136 μ . It consists of a pair of cartilages lateral to the nerve-cord. Their bases do not reach the notochord, and their thickness in transverse section is about 8 μ . The hæmal arches also consist of pairs of cartilages which do not reach up to the notochord. They are each about 16 μ thick, and are separated at their distal ends by about 16 μ of closely packed skleroblastic cells, which have not secreted any matrix as yet. Further forward the cartilages are considerably smaller, restricted to the sides of the caudal vein, and extend only through a length of about 30 μ . Posteriorly the skleroblasts between the distal ends of both dorsal and ventral pairs of cartilages have secreted a matrix, and in this way the pairs of cartilages have become

fused. Their proximal ends have grown till they now stand on the notochord.

The hypurals are now beginning to expand laterally at their proximal ends, so as to form a broad seat for the convexity of the upturned notochord, so that the thrust of the tail is more widely distributed. Fusion has taken place between the hæmal arch and radial (*r.*) described in Stage V. The epaxial elements behind the neural arches have undergone a certain amount of fusion, so that there is now a smaller posterior and a larger anterior cartilage. The caudal artery and vein are both forked at their posterior ends to pass round the large "ventral hypural," which is not arched, to admit of their passage between it and the notochord. Fig. 6 is a reconstruction of this stage from a series of transverse sections.

Stage VII (2.2 cm.) (fig. 7).—Long narrow cartilaginous pieces (*car.*) have now made their appearance, one dorsally to the two posterior neural arches and the three original (apparently now two) epiural apophyses described above, and another ventral to the most anterior hæmal arch. They give articulation to a dorsal and a ventral group of procurent lepidotrichia. From the shape and position of this ventral piece of cartilage, it appears possible that it may be the homologue of the two radials or hypural apophyses which appeared just behind it and underwent fusion with two hæmal arches. The anterior ends of both these new cartilages develop into two or three smaller and more or less separate cartilages. The anterior peg of the "ventral hypural" now extends between the proximal ends of the next anterior hypural, with which it eventually fuses, giving rise to the appearance in transverse section of a fusion of the halves of the arch themselves, and making in fact a small bridge, dorsal to the caudal artery and vein, which has rather a puzzling appearance.

The division between the halves of the "dorsal hypural" (*d.*, Pl. II. fig. 8) has now disappeared, or, in other words, the two uppermost hypurals have fused (Stage VIII), and a certain amount of absorption of the two large hypurals seems to be taking place, which, together with growths in other points, such as the posterior margins and the proximal ends, causes a considerable change in shape. Between Stages II and VII the rate of growth of the hypurals is greater than the rate of increase in girth of the notochord; but between Stages VII and X there is a reversal of this disparity which culminates in the condition where the notochord has the relatively enormous proportions so characteristic of the latest available postlarval stages of this fish. Stage VIII shows the first step in this inflation of the notochord, but here, as in later stages, the upturned tip or Chordastab is not affected. In this respect Teleosts show an important difference from Elasmobranchs (see Schauinsland, p. 462). Figs. 9 and 10 are drawn under the binoculars with camera lucida, and show a dissection of the posterior end of the notochord, nerve-cord, and cartilaginous elements of a fish 4.2 cm. long.

Fig. 9 is practically a lateral view and fig. 10 a dorso-lateral view. It will be seen that the posterior neural arches are much further developed than the anterior ones.

Reference to the adult fish (fig. 12) shows that the neural arch has, on each side, two points of attachment to the centrum, between which points the segmental nerve emerges. Examination of Stage IX proves that the primary point of attachment is the anterior one; the process of formation of the posterior one—as a backwardly directed spur (*sp.*)—can be seen in figs. 9 and 10. A comparison of these backwardly directed spurs with some cartilages described by Schauinsland in Hertwig's book (p. 467) shows that it is probable that they represent intercalaria.

Schauinsland says: "The bulk of the base of the arch (cartilaginous stage) is at the cranial end of the vertebra, but this base sometimes extends caudalwards (Pike). The caudal part may even be cut off to form a separate piece of cartilage (*e. g.* in the tail of the Trout). This," he considers, "should be looked upon, probably in the case of the Pike and pretty certainly in that of the Trout, as the remnant of the second arch and as homologous to the cranial arch of *Amia*" (*i. e.* it is formed by the cranial half of a sklerotome: for this reason it is on the caudal end of a vertebra).

Stage X.—The posterior edges of the three large hypurals (fig. 11, 4.5 cm.) have grown considerably, owing to additions from the large enveloping cap of skleroblasts (not shown in figure) on which the lepidotrichia are seated. The proximal ends of these hypurals have grown also with the notochord, so that a large gap (*g.* figs. 9–11) has appeared—and continually increases in size—between the dorsal and ventral hypurals. It will be noticed that the posterior neural arch is dividing into two.

The adult specimen I dissected was 16.5 cm. long. The centra are very "papery," and constrict the notochord only very slightly. The condition of the posterior neural arch is interesting. At first sight the penultimate centrum appears to be carrying two arches. Comparison with previous stages, however, shows that this is not so, but that the appearance is due to the fact that the division, incipient in Stage X, has now been completed. As a result of this, the segmental nerve, which in Stage IX emerged beneath the undivided arch, now lies in the cleft, and a secondary ossification *beneath* the nerve has finally reunited the two half-arches at their points of attachment to the centrum. Similarly, the hypural carried by this centrum has divided, and the two halves are covered by confusing secondary ossifications.

The double neural arch in *Pleuragramma antarcticum* and the arch immediately in front of it are considerably more expanded and better ossified than those in front of them.

The posterior part of the hypural borne on the penultimate centrum of *Pleuragramma antarcticum* has a thick, well-ossified, posterior edge, especially thick at the tip, while the rest of it is very thin and membranous. The hypural behind the one just

mentioned has similarly a thick, well-ossified, posterior edge and proximal portion, whilst the rest is very thin and membranous. The dorsal and ventral hypurals, which give attachment to the majority of lepidotrichia, are now widely divergent, thin, and membranous. These two, together with the hypural immediately in front, are ankylosed to the last centrum. Of the two epurals whose development I have traced above, the posterior one is well ossified and thick, while the anterior one has a thick, well-ossified posterior edge and a thin, membranous, expanded anterior edge. The upturned tip of the notochord is quite free and naked, reaching about halfway up to the anterior margin of the dorsal hypural (*d.*). The upturned nerve-cord also runs up to about this level, beyond which I have failed to trace it in the dissection I have made. The cartilaginous elements to which the fin-rays are attached have grown a good deal by this time, but have not become ossified.

SUMMARY.

1. The development of the vertebral column begins at the caudal end, the hypaxial elements being the first to appear. This coincides with a down-bending of the notochord (compare with this the analogous condition of the vertebral column in the Ichthyosauria). Epaxial elements do not appear until this condition has given way to the straight condition again. Arches appear as paired cartilages at the sides of the caudal artery and vein and of the nerve-cord. They are separated from the notochord by connective tissue.

2. The notochord is of a relatively enormous size, and persists with only slight constriction throughout life. The centra consist of thin papery lamellæ of membrane-bone. Ossification is generally weak.

3. The neural and hæmal arches of the penultimate centrum are double, owing to the splitting of single rudiments. Similar phenomena are to be observed in other fishes. They may be produced by different causes:—

- (1) Splitting of an originally single rudiment.
- (2) Crowding of two arches on to one centrum.
- (3) Fusion of the first epidual apophysis with the last neural arch.
- (4) Exceptional equal development of both arch and intercalary.
- (5) Secondary diplospondyly, *i. e.* fusion of two centra.

4. Large cartilages are present above and below the last two centra in the adult, which support a dorsal and a ventral series of procurent fin-rays. Their great size is probably connected with the weakness of general ossification.

5. The hypural bones of the adult are formed by a fusion of hæmal arches and radials. This compound nature of the hypurals

may be seen anteriorly in adult Selachians and in the Sturgeon, but it has not been shown before, as far as I am aware, in Teleosts.

BIBLIOGRAPHY.

(See O. Hertwig, 1906. Jena. Entwicklungslehre der Wirbeltiere, Bd. III. Teil 2, Kap. vi. pp. 456-82.)

- STANNIUS. 1854. Handbuch der Anatomie der Wirbeltiere, 2 Aufl. 1854. (Siebold u. Stannius, Handbuch d. Zootomie, Theil ii. Heft i. Berlin, 1854-56.)
- A. KÖLLIKER. 1860. Ueber das Ende der Wirbelsäule der Ganoide und einiger Teleostier. Leipzig.
- LOTZ. 1864. Ueber den Bau der Schwanzwirbelsäule der Salmoniden, etc. Zeitschr. wiss. Zool. Bd. xiv.
- GRASSI. 1883. (Développement de la colonne vertébrale chez les poissons osseux. Archiv. Ital. biologie, t. iv. 1883.) Lo sviluppo della colonna vertebrale ne pesci ossei. Reale Accad. dei Lincei, ser. 3, Memorie, vol. xv., 1882-83.
- SCHEEL. 1893. Beiträge zur Entwicklungsgeschichte der Teleostierwirbelsäule. Morphol. Jahrb. Bd. xx. Leipzig.
- v. EBNER. 1896. Ueber die Wirbel der Knochenfische und die Chorda dorsales der Fischer und Amphibier. Sitzungsber. d. k. Akad. d. Wiss. Wien, Math.-Nat. Kl., Bd. cv.
- USSOW. 1900. Zur Anatomie und Entwicklungsgeschichte der Wirbelsäule der Teleostier. Moskva, Bull. Soc. Nat., n. s. xiv. p. 175.
- ALBRECHT. 1902. Zur Ent. des Achsenskelettes der Teleostier. Inaugural-Dissertation d. math. und nat. Fak. d. Kaiser-Wilhelms-Univ. zur Erlang. d. Doktorwürde. Strassburg.
- A. AGASSIZ. 1878. On the Young Stages of some Osseous Fishes. Boston, Mass., Proc. Amer. Acad. Arts Sci. vol. xiii. p. 117.
- T. H. HUXLEY. 1859. Q. J. M. S. vol. vii. p. 41.
- J. A. RYDER. 1884. Washington, D.C., Rep. U.S. Comm. Fish. p. 1057.
- R. H. WHITEHOUSE. 1910. Caudal Fin of Teleostomi. P. Z. S. p. 590.
- C. T. REGAN. 1913. Trans. Roy. Soc. Edinb. xlix.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. Tail end of a specimen of *Pleurogramma antarcticum*, 8 mm. long. The specimen was stained, cleaned, and mounted whole in Canada balsam. The skleroblastic tissue, *sk*, is represented semidiagrammatically by dots. Notice the down-bending of the tip of the notochord.
2. Tail end of a specimen of *P. antarcticum*, '85 cm. long. Camera-lucida sketch from a whole mount. Notice down-bending of the tip of the notochord, the formation of definite cartilaginous elements, *a'*, *a''*, by the skleroblastic tissue, and the appearance of lepidotrichia, *lp*.

- Fig. 3. Camera-lucida sketch of the tail of a specimen of *P. antarcticum*, 1.05 cm. long. Notice the appearance of skleroblastic tissue, *sk'*, dorsal to the notochord, accompanied by a slight up-bending of the tip of the notochord. *a*, a fusion of cartilages marked *a'* and *a''* in fig. 2. *b*, a hæmal arch. *c*, a radial.
4. Tail of a specimen of *P. antarcticum*, 1.3 cm. long. Definite cartilaginous elements, *ep*, have been formed dorsal to the notochord, which has now a marked dorsal flexure. Notice the row of lateral-line sense-organs extending on each side along the trunk and on to the dorsal fin, marking its future mid-line. *phy*, posterior hypural. *k*, an abnormal piece of cartilage.
 5. A whole mount of the tail of a specimen of *P. antarcticum*, 1.55 cm. long. The dorsal flexure of the notochord has reached its maximum. Neural arches, *na*, have begun to appear. The figure shows three stages in the formation of a hypural. Anteriorly there is a hæmal arch, behind it is another hæmal arch with a radial, *r*, at its distal end. The two elements have not begun to fuse. Behind these again is a hypural (for description of which see Stage III).
 6. A reconstruction from a series of sections of the tail of a specimen of *P. antarcticum*, 1.8 cm. long. (Sections posterior to "dorsal hypural" lost. Tip of notochord and nerve-cord hypothetical.) The cartilaginous elements are represented as seen in a section near the sagittal plane. Notice the fusion that has taken place between radial and hæmal arch seen in fig. 5.
 7. A reconstruction from a series of sections of the tail of a specimen of *P. antarcticum* 2.2 cm. long. Notice the anterior peg, *p*, of the "ventral hypural" which passes between the notochord and caudal vein and artery, fusing with the proximal portion of the hypural in front of it. Notice also the cartilaginous elements, *car*, which later on give attachment to the anterior dorsal and ventral procurent fin-rays. An asterisk marks the exit of the caudal artery and vein from the hæmal arches.

PLATE II.

- Fig. 8. A dissection of an "odd tail" of *Pleuragramma antarcticum*, probably 2.8 cm. long. It shows the uniform nature of the "dorsal hypural," *d*, (the compound nature of which has been seen in previous figures). It will be noticed that the posterior neural arch, *n*, is expanding at its distal extremity.
9. An antero-lateral view of a dissection of the notochord and cartilaginous elements of the posterior end of a specimen of *P. antarcticum*, 4.2 cm. long. It was drawn under Zeiss binoculars with the aid of a camera lucida. Note the increase in development of the neural arches from before backwards. The sketch illustrates the way in which the neural arches grow over the segmental nerves. *sp*, backward growing spurs. *g*, gap between dorsal and ventral hypurals.
 10. A latero-dorsal view of the specimen figured above (fig. 9). It will give a better idea of the shape of the neural arches. *e, f*, the two halves of a neural arch.
 11. A camera-lucida sketch of a dissection (mounted in balsam) of the notochord and cartilaginous elements of the posterior end of a specimen of *P. antarcticum* 4.5 cm. long. Notice the incipient division of the posterior neural arch into two. A considerable change in the shape of the two large hypurals has taken place (see text, p. 257).
 12. A dissection of an adult specimen (16.5 cm.) of *Pleuragramma antarcticum*. The tip of the notochord is represented as being naked. The attachment of the large hypurals is rather broken in this specimen (it had been devoured by a Seal), so that it is quite possible that the tip of the notochord was ensheathed by thin membranous bone. The drawing was made with the help of a camera lucida and Zeiss binoculars. *d*, posterior or dorsal hypural. *a*, anterior or ventral hypural.
 13. A dissection of a specimen of *Trematomus newnesii*, 6 cm. long (adult?). It is given for comparison with fig. 12. The tip of the notochord is naked and extends out between the caudal fin-rays.
 14. A diagram of the caudal skeleton of *Trematomus borchgrevinkii*.